



Litter species richness and composition effects on fungal richness and community structure in decomposing foliar and root litter



Eveli Otsing^{a,*}, Sandra Barantal^b, Sten Anslan^a, Julia Koricheva^b, Leho Tederso^{a,c}

^a Institute of Ecology and Earth Sciences, University of Tartu, 14A Ravila, 50411, Tartu, Estonia

^b School of Biological Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, UK

^c Natural History Museum, University of Tartu, 14A Ravila, 50411, Tartu, Estonia

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ABSTRACT

Litter species richness influences fungal diversity because of resource heterogeneity. Litter species composition effects on decomposition have been studied mostly in aboveground litter. However, little is known about the effects of litter diversity of roots and litter type effect on fungal diversity in general. We addressed litter species composition and richness effects on diversity of ectomycorrhizal (EcM), saprotrophic and pathogenic fungi in decomposing foliar and root litter in the Satakunta forest diversity experiment by varying litter species richness from one to four species in 560 litter bags incubated under tree canopies. After one year of decomposition, there were no significant non-additive effects of litter mixtures on mass loss. Litter species composition was the strongest predictor for saprotroph and plant pathogen community structure in foliar litter, but its effect on root litter fungal composition was much weaker. Litter diversity strongly enhanced fungal richness in foliar but not in root substrate. We found no evidence for host litter preferences in host-specific EcM fungi. Our study suggests that litter species richness and especially certain litter species may influence decomposition through modifying fungal community composition both in foliar and root litter.

1. Introduction

Functioning of above- and belowground components of terrestrial ecosystems are influenced by feedbacks between plants, root associated organisms and decomposers (Wardle et al., 2004). In mixed forest ecosystems, individual trees affect decomposition directly through species-specific litter quality (McClaugherty et al., 1985; Hobbie, 1992; Silver and Miya, 2001) and indirectly through modified micro-environmental conditions and soil biota composition (Joly et al., 2017). In particular, Hobbie et al. (2006) showed that tree species identity affects decomposition via both litter chemistry and effects on soil temperature. The strength of feedback to plants depends on plant traits and interactions between root- and litter-associated microbes (Cairney and Meharg, 2002; Ke et al., 2015).

Together with environmental variables such as temperature and moisture, plant traits such as leaf nutrient and lignin concentration are strong predictors of litter decomposition in forest ecosystems (Hättenschwiler, 2005; Cornwell et al., 2008; Bani et al., 2018). Due to litter quality effects, broadleaf litter is expected to decompose faster than coniferous litter (Prescott et al., 2000). Plant litter is often decomposed more rapidly in the vicinity of the mother plant due to

specialized decomposer community, termed as ‘home-field advantage effect’ (Ayres et al., 2009; Veen et al., 2015). Home-field advantage has been found to be common in forest ecosystems and may cause an average 8% faster litter mass loss in ‘home’ than ‘away’ habitats (Ayres et al., 2009). Home-field advantage in decomposition communities has been found to be related to chemical similarity in litter quality rather than related to associations between specific species (Gholz et al., 2000; Veen et al., 2015). Ke et al. (2015) showed that litter decomposability through soil nitrogen (N) availability may determine the strength of plant-soil feedback in communities dominated by arbuscular mycorrhizal fungi.

In forest ecosystems, foliar litter from different plant species becomes usually mixed because of wind and roughly simultaneous litter fall in the autumn (Staelens et al., 2003; Ľupek et al., 2015). Similarly, root litter is mixed, because roots of plant species commonly intermingle and their turnover is usually synchronous (Fogel, 1983; Brassard, 2010). Most root systems of trees in boreal forest ecosystem have been shown to stop activity after leaf-drop in the fall (Burke and Raynal, 1994). Mixing litter of different plant species may cause shifts in microbial communities that may affect decomposition rates (Chapman et al., 2013). In particular, chemically diverse litter mixtures

* Corresponding author.

E-mail address: eveli.otsing@gmail.com (E. Otsing).

provide decomposers with a varied diet that has strong effects on microbial communities and functional diversity and hence may increase or decrease decomposition rates with positive or negative feedbacks to plants (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Decomposition patterns of leaf litter mixtures are usually ‘non-additive’, i.e. not directly predictable based on the biogeochemical processes in parent litter, whereas ‘additive’ responses in mixtures are predictable from component species (Gartner and Cardon, 2004). Most studies have revealed that litter species composition has a stronger effect on decomposition rates than litter richness *per se* (Wardle et al., 2006; Hoorens et al., 2010; Cuchietti et al., 2014; Handa et al., 2014; Setiawan et al., 2016).

Litter mixing affects microbial abundance and community structure and tends to result in synergistic or antagonistic effects where decomposition rates are faster or slower, respectively, than expected based on decomposition rates of litter of component species (Gartner and Cardon, 2004). However, linking microbial community changes directly to these non-additive patterns in litter mixtures has been elusive (Chapman et al., 2013). It has been shown that litter species composition determines the direction of non-additive effect in the litter mixture (De Marco et al., 2011). It has been suggested that synergistic effects in litter mixtures are caused by fungi-driven nutrient transfer from higher quality litter to the poor one, and antagonistic effects are due to release of inhibitory compounds (Chapman et al., 1988). Berglund and Ågren (2012) showed that the litter mixture decomposes faster than parent litters alone when the litter of the higher quality mineralizes nitrogen fastest. More diverse and patchy plant litter may promote niche specialists and hence support higher microbial diversity (Kubartová et al., 2009; Chapman and Newman, 2010; Santonja et al., 2017). Litter of different tree species develop distinct microbial communities, however, microbial changes may not translate to predictably altered litter decomposition (Aneja et al., 2006; Chapman and Newman, 2010).

Root litter represents an important carbon (C) source for microbial communities (Rasse et al., 2005) and plays a substantial role in plant-soil feedback (Freschet et al., 2013). Due to lower nutrient concentration and higher lignin content, roots are considered to be more recalcitrant than foliar litter and this might have an effect on their microbial degradability (Berg and McLaugherty, 2014; Jacobs et al., 2018). To date most studies on litter decomposition have focused on the foliar component and little attention has been given to understanding the patterns and drivers of the large source of carbon that is found in roots, partly because of the challenges of studying belowground litter. Little is known about the community composition of microbial decomposers of dead roots. For example, Herzog (2017) and Kohout et al. (2018) studied the composition of dead root associated decomposer communities over a two-year period; Fisk et al. (2011) investigated fungal community development on dead roots in disturbed rhizosphere conditions. Several studies have been conducted to analyze if fungal community composition varies between litters of different diversity (Kubartová et al., 2009; Chapman and Newman, 2010; Chapman et al., 2013). However, the effects of foliar litter diversity and particularly root litter diversity on fungal functional groups in forest ecosystems remain largely unknown.

Saprotrophs, endophytes, plant pathogens and EcM fungi are the major fungal guilds inhabiting foliar and root litter (Lindahl et al., 2007; Voříšková and Baldrian, 2013; Kohout et al., 2018). While saprotrophic fungi are the primary decomposers of C-rich biopolymers (Cooke and Rayner, 1984; Talbot et al., 2013), some plant pathogens (Baker and Bateman, 1978; Osono, 2007) and endophytes (Müller et al., 2001; Korkkama-Rajala et al., 2008; Kohout et al., 2018) are also potentially important in the initial stages of decomposition, as they often express saprotrophic activity after leaf senescence. EcM fungi take part in organic matter decomposition through mobilizing organically bound nitrogen (Lindahl and Tunlid, 2015), which may lead to direct competition for resources with saprotrophs and result in an overall decrease in decomposition rate (Fernandez and Kennedy, 2016).

Host preference has been observed in endophytes, plant pathogens, saprotrophs and mycorrhizal fungi (Molina et al., 1992; Zhou and Hyde, 2001; Pöhlme et al., 2018). Of these four groups, mycorrhizal fungi exhibit a high degree of host specificity which is thought to be a result of their coevolution with plants (Brundrett, 2002). Thus, the diversity of belowground organisms who are intimately associated with plant roots (e.g. EcM fungal taxa) are predicted to create stronger aboveground effects (influence on plant productivity, composition, and diversity) compared with saprotrophs with low specificity (Wardle et al., 2004). Also, community composition of EcM fungi might respond strongly to the aboveground communities through litter chemistry (Conn and Dighton, 2000). Tedersoo et al. (2008) showed that EcM fungal community composition in dead wood responds to tree species of woody litter that probably results from chemical differences in substrate. Given the specialization of many EcM fungal species to certain plant host genera (Kennedy et al., 2015; Molina and Horton, 2015), we predict that the relative proportion of host-specific EcM fungi is greater in their host plant's litter than in other tree species' litter due to their long evolutionary history of being exposed to the host plant's litter.

The aim of this study was to determine the ecological relationships between fungal diversity and plant diversity via feedbacks to foliar and root litter. We hypothesized that mass loss rate increases with increasing litter diversity (H1); litter from a single tree species decomposes more rapidly under the trees where it originated (H2); composition of saprotrophs, plant pathogens and EcM fungi is mainly driven by litter species composition (H3); litter species richness enhances fungal richness (H4); and the relative proportion of host-specific EcM fungi is greater in the litter of their intimate host plant (H5).

2. Materials and methods

2.1. Study site and experiment set up

To study litter diversity effects on fungal community composition and richness, a litter decomposition experiment was set up in the Satakunta forest diversity experimental area (www.sataforestdiversty.org) in Finland (61.714°N, 21.983°E). The forest diversity experiment was established in 1999 to study the effects of tree species richness and composition on ecosystem functioning. Experimental plots in three different areas were planted with monocultures, two-, three- and five-species mixtures of silver birch (*Betula pendula*), black alder (*Alnus glutinosa*), Siberian larch (*Larix sibirica*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Each 20 m × 20 m plot contains 13 rows with 13 trees per row planted at 1.5 m intervals. In mixed species plots, all tree species were planted in equal proportions. In 2013, one replicate of each treatment per area was thinned with tree density reduced by half. According to the data of Pori meteorological station, in 2014–2015, the annual precipitation was 567–673 mm and annual temperature was 6.7–6.9 °C (www.ilmatieteenlaitos.fi).

In order to minimize spatial effects, we selected two five-species mixture plots (plots 18 and 22 in area 1) to test the effects of tree species identity, foliar and root litter species composition and richness on microbial diversity and litter mass loss. Our block design included 20 tree individuals per plot with a total of 40 focal trees (blocks). Within each of the two plots, we randomly selected 5 individual trees of each tree species except the non-native larch and placed litter bags (see next paragraph) under these trees. Each tree (block) received eight bags of single-species foliar and root litters, two bags of two-species (the same random combination for both foliar and root litters) and two four-species foliar and root litter mixtures. In each block, we used two extra bags of single-species foliar and root litter to increase the power for ‘home’ versus ‘away’ comparisons.

Foliar litter was collected by use of litter traps from neighboring monoculture plots and air-dried at room temperature in September, 2014. Roots of the four tree species were excavated from the edges of the two selected plots in order not to disturb the rest of the plot. We

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